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ODONATE BIONOMICS: I—NOTES ON THE FOOD
OF DRAGONFLIES. 1. ODONATA VS.
ANTS AND BEES.

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Various species of dragonflies have been collected which were found to have the mouthparts of ants or bees attached to their legs. How these insects became so attached has remained largely a matter of conjecture, however, since apparently no one has observed an engagement which resulted in this state of affairs. A few authors have reported cases of dragonflies feeding on ants. Butler (1915) described the decimation of a flight of ants by several species of dragonflies, but collected no specimens, leaving unknown the identity of the insects involved. Lamborn (1922) refers to an unnamed species of Odonata catching worker ants in Nyassaland, and Hobby (1936) cites both sexes of the cosmopolitan *Pantala flavescens* as "eating bodies only of winged Formicidae" in Coimbatore, India. In none of these cases were specimens of the dragonflies with their prey obtained, and only in the last-named instance is specific identification of the dragonflies made. Although a number of accounts have been published which enumerate the food of various species of dragonflies, so little accurate observation has been made of the actual feeding habits of adult dragonflies that discussion of the subject necessarily involves a certain amount of speculation. One of the purposes of this paper is to stimulate interest in the feeding habits of dragonflies, and all observations will be gratefully received by the author.

There are two questions which should be dealt with before attempting to explain the occurrence of dragonflies with the mouthparts of other insects attached to their legs. What role do the legs of an adult dragonfly play in the capture of its food? How much discrimination do these insects exercise in the selection of their diet?

It has been generally supposed that dragonflies scoop their flying prey out of the air by forming a "basket" of the legs, drawing them up under the head. Hobby (1933) gives a comprehensive account of dragonfly feeding and states "Smaller insects are probably taken directly in the mouth . . . larger ones are secured by the long legs which hang below to form a 'capture-net.'" Sharp (1895) says "We believe that the legs are of great importance in capturing the prey, they being held somewhat in the position shown. . . ." and gives an adequate figure. Sharp also goes on to give a detailed and illuminating account of the feeding of Odonata in which he again states that the legs, rather than the mouth, are probably the primary instrument of capture, but that the transfer of prey to the mouth occurs so rapidly as to be virtually unobservable. But quite contrariwise, Montgomery (1925) reports the following personal observation. "A number of dragonflies were hawking in an open space in the woods. Three taken were all different species, *Aeschna constricta*, *A. umbrosa*, and *Anax junius*. I spent about two hours watching them catch Diptera. As a dragonfly approached a small insect it checked its speed slightly and drew its head upward and backward until the mouth was in an anterior position. The prey was caught in the mouth and the mouthparts were seen to move rapidly as the dragonfly flew on leaving a vacant space where a small insect had been seen a moment before." If this observation is accurate, it bears out a remark made by Sharp (1895) in a passage preceding the one quoted above, where he states "it is believed that the mouth is largely instrumental in the capture, though the flight of these insects is so excessively rapid that it is difficult, if not impossible, to verify the action of the mouthpieces by actual observation." This statement is rather inconsistent with Sharp's more detailed account of the feeding of Odonata which stresses the importance of the legs, but, withal, his account is one of the most thorough in the literature. It is the experience of the present author that valid observations on the feeding habits of dragonflies are so difficult to make that only a stroboscopic camera could yield completely reliable results.

From the foregoing it is apparent that some dragonflies may capture their prey by means of the legs alone while others employ only the mouthparts, and that the use of both legs and mouthparts is the most likely procedure. However, it has not yet been shown that any species confines itself entirely to any of these habits. The large, rapacious species like *Tachopteryx thoreyi* and *Hagenius brevistylus* often capture and subdue insects almost as large as themselves, a feat which they could hardly accomplish without the

use of the legs. Calvert (1893), without stating how the food is captured, writes "The first pair of legs are usually employed to hold the food as it is devoured." This is particularly true of these savage species which must devour their prey piecemeal. It certainly agrees with the present author's observation of *Hagenius brevistylus* in New Jersey, where one was seen to capture and devour a mature *Libellula incesta*, perching on a dead branch with the two posterior pairs of legs and using the first pair to hold and manipulate the prey while it was being eaten. Another large gomphine, a new species from Florida not yet described, was also seen to overpower and eat a female *Libellula incesta* in identical fashion, and in this case there was very little difference between the size of the hunter and that of the victim. It is obvious that such captures could not have been made with the mouthparts alone.

It is probably only when the prey is small and weak in proportion to its captor that the legs are not used. The writer has seen *Enallagma aspersum* in New Jersey, catching tiny white flies, apparently without using its legs; and he has also seen fairly large crane-flies captured by *Didymops transversa*, which flew with its remarkably long legs plainly extended downward and not drawn up under the mouth. Brues (1946) cites a New Zealand species, *Somatochlora smithii*, which has been seen to dive into the water, immersing its head, to capture midge larvae or pupae. Various North American dragonflies, especially those of the genus *Stylurus*, are often seen to plunge into the water. Williamson (1934) gives a typical account, but neither he nor any other author has discovered why these insects do so; it remains unknown whether they dive for food, drink, or pleasure. The present writer seriously questions the accuracy of Wilson's account and interpretation quoted by Needham and Heywood (1929, p. 101).

It is the conclusion of the author that in most cases dragonflies capture their prey by using legs and mouthparts together, the legs being used at least to guide and stuff the prey into the open mouth which also assisted in the capture. Occasionally a dragonfly may use legs or mouth alone, but this does not seem to be the normal procedure. It is quite obvious, then, that an ant or bee, if captured by a dragonfly, would sometimes have an opportunity to seize its captor by the legs, something it could not do if mouth alone were used, especially in the case of a wingless ant which must be picked up from the ground or from vegetation.

The diet of Odonata is notoriously diverse, many species devouring almost any insect which they are able to subdue and which is soft enough for them to chew up. Williamson (1900) remarks

"Of the insects eaten diptera are more preferred than any other order, though all soft bodied insects seem to fall prey to their ravenous appetites." This is borne out by Campion (1914, 1921), Hobby (1933, 1936), and Poulton (1906), whose reviews of dragonfly food show that Diptera are more favored than all other orders combined. Ants are rather hard-bodied, however, and it seems that they do not form an important part of any dragonfly's fare. Indeed, the only definite case of ants being eaten which is cited in any of the five papers just referred to is the one mentioned by Hobby (1936) who quotes a correspondent regarding *Pantala flavescens* eating winged ants in India. Though the reviews of Campion and Poulton cite insects of many orders as food of Odonata, they include no Formicidae. The latter author states, "Short as it is, the list is extremely interesting, and raises the expectation that Dragonflies will be found to prey rather largely upon specially defended groups of insects. Bequaert (1930), in a study of the enemies of ants, cites only two cases of ants being eaten by dragonflies. They are those reported by Butler (1915) and Lamborn (1922). If dragonflies prey only incidentally on specially protected insects, it is significant that Bequaert (loc. cit.) reaches the conclusion that ants are not specially protected to any great extent.

Assuming that there is an actual preference for soft bodied insects (Hobby, 1933), it is possible that a dragonfly, despite its reputedly superior vision, would fail to recognize an ant or beetle as unsuitable for food until it was in its grasp. In such a case it would probably drop the undesirable victim unless, as in the case of an ant, it were first seized by it. Instances of such rejections have not been reported, though Williamson (1932) makes the following remarks about *Boyeria vinosa* in Missouri. "Its food so far as observed consists of minute and usually aquatic insects which it captures with a bobbing-in-and-out flight about logs, trash, and overhanging nooks, usually along the course of a stream. It discriminates in its food, rejecting some insects after approaching very near to or seizing them. Instances of this were not infrequent but the distance always prevented determining certainly whether the rejected insect was seized or not." Here the question arises of a dragonfly learning what food is suitable and remembering in some way to reject unsatisfactory insects, though Hobby (1933) points out that some prey may escape for reasons of size, rather than being deliberately rejected. In spite of Williamson's observation, just quoted, most of the evidence points to the truth of the statement made by Brues (1946) that "dragonflies have not developed specialized dietaries" and will try to eat anything of suitable size and abundance. That

no large group of dragonflies discriminates against ants or other unsuitable food is suggested by the following specific cases which fall into six different families of Odonata.

Williamson (1918) made the following remarks about a very small gomphine, *Archaeogomphus hamatus*, from Colombia. "One female specimen has the head of a bee attached to the left hind tibia. The apex of the tibia is broken off, the mandibles of the bee gripping the tibia firmly near its base. Through the kindness of Mr. Currie this specimen was submitted to Mr. J. C. Crawford of the United States National Museum who reports that 'the head is that of one of the stingless honeybees, *Trigona* sp. These bees, of which there are many species in the tropics, are social in their habits, and build nests, combs, etc., and store honey. It is possible that the dragonfly was attacked by the bee when in the vicinity of its nest, but more probably the dragonfly captured the bee which seized its captor by the leg before being dispatched.'" Dragonflies have been frequently cited by apiarists as predators upon their domestic honeybees. Bromley (1948), Clausen (1940), Goodacre (1923), Hobby (1933, 1936), Johnson (1899), Needham and Heywood (1929), and Wright (1944) are among the writers who have discussed bee-eating Odonata. In the New World, the most destructive dragonfly to bees is *Coryphaeschna ingens*, often called the "bee butcher," while in Europe *Aeshna cyanea* and *Brachytron pratense* cause serious losses to beekeepers. These are all large, powerful insects, so it is interesting that bees are also attacked by the tiny *Archaeogomphus*. This case is also of interest because it may be the only recorded instance of a bee's mouthparts being found attached to any species of Odonata. The suggestion that the dragonfly might have been attacked by the bee is plausible in view of the former's relatively small size and this opens a new line of inquiry. There are no records of bees' mouthparts being found attached to any of the large species noted for their depredations on honeybees, and this suggests that the bees may be caught and devoured by the dragonfly without the use of its legs, giving the bee no opportunity to seize them.

Another interesting case was recorded by Montgomery (1932) who captured in Indiana a male of *Tachopteryx thoreyi* which had the head of an ant attached to the tarsus of the second left leg. This ant was identified as *Camponotus herculeanus pennsylvanicus* De Geer by F. M. Gage. It seems likely that the head is that of a wingless worker since such forms greatly outnumber the winged sexual forms which occur only occasionally. Of course, it is difficult to determine the sex of an ant from the mandibles alone, so no

definite statement can be made whether the ant was a winged form or a worker. While Lamborn (1922) did cite workers as food of dragonflies, the few other authors who had anything to say referred only to winged ants. Perhaps this is because the mass mating flights of ants are conspicuous and their invasion and decimation by dragonflies would be more often noted than the capture of a solitary wingless individual.

Byers (1927) mentions a female of *Enallagma laurenti* to which an ant, *Darymyrmex pyramicus*, was attached. Williamson (1922) cites a male of *Enallagma cardenium* from Florida which has the head of a male *Pseudomyrma* sp. attached by the mandibles to the left middle tarsus. Male ants of this genus are all winged and most of the species are arboreal, according to F. M. Gaige, so it may have been seized while in the air or while running over vegetation. Williamson (1922) also mentions another ant of which head and thorax were attached to one of the legs of a *Hetaerina laesa* from British Guiana. Dr. Gaige identified this ant as a minor worker of *Pheidole* sp. and stated that many species of *Pheidole* forage on vegetation to the height of several feet and that they are "pugnacious little devils." Williamson goes on to say "Such an ant might conceivably seize a resting dragonfly by its legs, but I have little doubt that the dragonfly was the aggressor and that it plucked the ant from its perch, and the ant retaliated by seizing a leg in a death grip."

In the experience of the present writer, two species of Odonata have been collected in Pennsylvania with the mandibles of ants attached. One of these, a female of *Aeshna tuberculifera*, has the entire head of a *Camponotus* affixed to the right front tarsus at its base. The other, a female of *Libellula semifasciata*, has the mandibles of a large ant, probably *Camponotus*, attached to the extreme distal end of the left middle tibia. The chewed condition of this latter ant's head indicates that the dragonfly made more than a little effort to disengage it.

In the case of *Archaeogomphus*, it is quite reasonable to suppose that the bee was caught by the dragonfly while the former was in flight, but in the instances of *Tachopteryx Aeshna*, and *Libellula* it seems unlikely that the ant was a winged form in every case. How, then did the wingless ants manage to attach themselves to the dragonflies? Did they attack the dragonflies while they rested or did the dragonflies capture the ants while they ran along the ground or over the vegetation?

The habits of *Tachopteryx thoreyi* are well known and it has often been reported that its normal food includes moths, butterflies,

and other dragonflies, taken on the wing. The prowess of *Tachopteryx* at capturing such large prey has been frequently acclaimed, but it is unlikely that this insect would often seek out so small and elusive a quarry as an ant, unless hard pressed by shortage of its usual food. Nevertheless, it is even more unlikely that even the most ferocious ant would seize the leg of a *Tachopteryx* while it rested on a tree trunk unless the dragonfly attempted to catch a passing ant. This latter possibility is so remote that it is reasonable to conclude, assuming the ant wingless, that the flying *Tachopteryx* caught the ant as the latter ran across a leaf or some similar exposed situation. Swynnerton (1936) cites a dragonfly, *Cacergates leucostictus*, as searching the backs of animals and men in Africa for tsetse flies. This shows how it is quite possible for dragonflies to pick up their victims from the ground or from the vegetation, though such a performance has been noted but rarely.

In the case of *Aeshna tuberculifera*, the normal food of this species corresponds to ants in size, if not in other characteristics. It has been generally concluded that the food of most species of *Aeshna* consists largely of small, soft-bodied Diptera and Hemiptera. They undoubtedly vary this diet considerably but few instances of the exceptional voracity displayed by *Tachopteryx*, *Hagenius*, *Anax*, and similar species have been pointed out. The writer has often seen individuals of *Aeshna umbrosa* flying about close to the foliage of trees and bushes, hesitating here and there as if about to alight but never alighting. It was impossible to determine whether or not *umbrosa* was intent upon catching insects on the leaves, but, if such were the case, it is altogether likely that some ants were being caught and that these would occasionally include species large enough to seize the dragonfly's leg and maintain their hold. Certainly, if the dragonfly were pursuing its supposedly normal diet of Diptera, it would confine its attention to the open spaces where mosquitoes, gnats, and midges dance about in throngs. Walker (1912) has mentioned this tree-searching habit of a species of *Aeshna*, but does not consider the possibility that ants were being caught.

Libellula semifasciata, often a woodland dweller, has food habits which make the presence of the ant's mandibles more easily explainable. In woodland clearings, in the early springtime, *semifasciata* is often seen flying about close to the vegetation, dipping down to a leaf from time to time, catching small insects; so it is to be expected that a few ants would be caught.

In the case of the small Zygoptera such as *Enallagma*, most species of which pursue their prey over the water, the best explanation

is that an aggressive ant affixed itself to the damselfly's leg while the latter insect was at rest. Even though this is in disagreement with Williamson's views quoted previously, the present author's observations are that the food of the smaller Zygoptera consists largely of minute Diptera which are usually so abundant about aquatic habitats that the capture of a suitable small winged ant would be a rare occurrence.

It has been suggested that ants attack teneral dragonflies soon after emergence. Indeed, Calvert (1913) mentions a specimen of *Tetragoneuria*, arrested in transformation, which was collected while still alive, but which had the last five segments of the abdomen more or less destroyed by ants. In such cases, however, the legs of the dragonfly are so poorly chitinized that they would be completely severed by a strong-jawed ant, and the dragonfly's mouthparts would be far too soft to make any impression on the ant's hard integument. This fate cannot befall a very great percentage of emerging Odonata since the majority of transformations takes place on emergent vegetation or in other situations often inaccessible to ants. In all probability, most of the dragonflies which are attacked by ants while teneral perish without offering much resistance.

CONCLUSIONS.

Because of conflicting statements of various authors cited, and the lack of reliable information on important points, few positive conclusions can be reached. However, the evidence points to the following generalities:

1. Dragonflies generally employ the legs to some extent in capturing their prey, though mouth alone is sometimes used to secure insects too small to be caught by the legs.

2. That dragonflies favor no particular pair or pairs of legs in capturing their prey is shown by specific cases of mouthparts attached to legs of all three pairs.

3. They have not been shown to avoid any group of insects in their dietary, and may be expected to prey upon ants and bees in proportion to their abundance.

4. Therefore the occurrence of dragonflies with the mouthparts of ants and bees attached to their legs can best be attributed to defensive seizure by these insects of the legs of their captors.

5. There is some evidence of an occasional offensive seizure of a dragonfly's leg by an ant or bee, especially in the case of small, delicate species such as *Enallagma*.

6. The inadequacy of information on this subject indicates the

need for much careful observation of the feeding of Odonata, and accurate reporting of factual data pertaining thereto.

REFERENCES

- Bequaert, Joseph** 1930. Are ants better protected against the attacks of their predaceous enemies than other Arthropods? *Zoologischer Anzeiger*, 88: 163-176.
- Bromley, S. W.** 1948. Honey-bee predators. *Journ. N. Y. Ent. Soc.*, LVI: 195-199.
- Brues, Charles T.** 1946. *Insect Dietary*. Cambridge, Mass., Harvard University Press.
- Butler, Amos W.** 1915. Dragonflies devouring winged ants. *Ent. News*, XXVI: 37.
- Byers, C. Francis** 1927. *Enallagma* and *Telagrion* from Western Florida. *Annals Ent. Soc. Amer.*, XX: 385-392.
- Calvert, Philip P.** 1893. Catalog of the Dragonflies of Philadelphia. *Trans. Amer. Ent. Soc.*, XX: 152a-272.
- 1913. *Ent. News*, XXIV: 431-432.
- Campion, Herbert** 1914. Some Dragonflies and their prey. *Ann. Mag. Nat. Hist.*, (8) Vol. 13: 495-504.
- 1921. Some Dragonflies and their prey—II. *Ann. Mag. Nat. Hist.*, (9) Vol. 8: 240-245.
- Clausen, Curtis P.** 1940. *Entomophagous Insects*. New York, McGraw-Hill Book Co.
- Goodacre, W. A.** 1923. A Casual Enemy of the Bee. *Agric. Gaz. New South Wales*, 34: 373-374.
- Hobby, B. M.** 1933. The Prey of British Dragonflies. *Trans. Ent. Soc. South of England*, 8 (2): 65-76.
- 1936. Dragonflies and their prey. *Proc. Roy. Ent. Soc. London*, B, 11: 101-103.
- These two papers contain important bibliographies.*
- Johnson, Charles W.** 1899. *Ent. News*. X: 219.
- Lamborn, W. A.** 1922. *Bulletin of Ent. Research*, XIII: 49.
- Montgomery, B. Elwood** 1925. Records of Indiana Dragonflies—I. *Proc. Ind. Acad. Sci.*, 34: 383-389.
- 1932. Records of Indiana Dragonflies—VI. *Proc. Ind. Acad. Sci.*, 41: 449-454.
- Needham, James G. and Heywood, Hortense B.** 1929. *Handbook of the Dragonflies of North America*. Springfield, Ill., Charles C. Thomas.
- Poulton, E. B.** 1906. Predaceous Insects and their Prey. *Trans. Ent. Soc. London*, 1906 (Part III): 398-401.

- Sharp, David** 1895. *The Cambridge Natural History*, Vol. V: Insects. London, MacMillan.
- Swynnerton, C. F. M.** 1936. *The Tsetse Flies of East Africa*. Trans. Roy. Ent. Soc. London, Vol. 84.
- Tillyard, R. J.** 1917. *The Biology of Dragonflies*. Cambridge, Cambridge University Press.
- Walker, Edmund M.** 1912. *The North American Dragonflies of the Genus Aeshna*. Univ. of Toronto Studies, Biol. Ser. No. 11.
- Williamson, E. B.** 1900. *The Dragonflies of Indiana*. Ind. Dep't. Geol. & Nat. Resources, 24th. Annual Report for 1899: 229-333, 1003-1011.
- 1918. Results of the University of Michigan —Williamson Expedition to Colombia, II. Occ. Papers, Mus. Zool., Univ. Mich., No. 59.
- 1922. Enallagmas collected in Florida and South Carolina by Jesse H. Williamson. Ent. News, XXXIII: 114-118, 138-144.
- 1932. Dragonflies collected in Missouri. Occ. Papers, Mus. Zool., Univ. Mich., No. 240.
- 1934. Dragonflies collected in Kentucky, Tennessee, North and South Carolina, and Georgia in 1931. Occ. Papers, Mus. Zool., Univ. Mich., No. 288.
- Wright, Mike** 1944. Some random observations on dragonfly habits with notes on their predaceousness on bees. Journ. Tenn. Acad. Sci., 19: 295-301.
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The Lepidopterist's Society: The first annual meeting of the Lepidopterist's Society was held December 29-30, 1950 at the American Museum of Natural History. At that time the Society was formally organized, with the adoption of a Constitution and By-Laws. The following officers were elected: J. H. McDunnough, President; A. H. Clark, Senior Vice President; W. Forster, K. J. Hayward, Vice Presidents; F. H. Rindge, Secretary; J. B. Ziegler, Treasurer. Members of the Executive Committee: H. Stempffer, T. N. Freeman, L. M. Martin, N. D. Riley, T. Shirozu, and J. G. Franclemont.

A number of papers were presented by members, including a symposium on "Geographic Subspeciation in Lepidoptera." Some painting, photographs, and exhibits, submitted by members in this country and abroad, were on display during the meetings.